

The Origin and Affinity of the Biota of the Kodiak Island Group, Alaska

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KODIAK ISLAND occupies an important biogeographical position. Situated along the northwestern border of the Gulf of Alaska, this island and its neighboring lesser islands have biogeographic relationships that radiate in three directions: westward along the Aleutian Islands, northward toward interior Alaska, and southeastward toward the temperate Pacific Coastal and Rocky Mountain regions of North America. The Aleutian and Bering Strait migration routes tend to funnel through this strategic area. Furthermore, the Island Group was probably severely glaciated during at least the later part of the Pleistocene. Karlstrom (1960) found geological evidence of a small late Pleistocene refuge on southwestern Kodiak Island. Nearly all subsequent biota, besides that which may have persisted on the refuge or on nunataks, would have had to originate as reinvaders from adjacent land or sea areas. A third peculiar feature in addition to location and glacial history is the possible significance of major habitat change caused by an encroaching timber line across the northeastern part of Kodiak Island.

A working hypothesis based solely upon geographic consideration could be proposed: that the biota of Kodiak Island is fashioned from elements of the three diverse regions with which it has geographic relationships. The purpose of this paper is to consider the relationship of the Kodiak Island Group biota to that of mainland Alaska. This should suggest what areas contribute heavily to the fauna and flora and indicate if geographic location is supported biogeographically.

A study of postglacial immigration of the Kodiak biota can be enlightening to the processes of intercontinental migrations, reinvasion following extermination, and centers of postglacial dispersion. The Bering land connection and the Aleutian chain of islands have been

migration routes from Asia. After Pleistocene glaciation, northwestern Alaska was a major reservoir of plants and animals to reoccupy nearly barren areas, as Kodiak Island is presumed to have been.

METHODS

Because the indigenous mammal and freshwater fish fauna is sparse, it is necessary to place major emphasis upon plants. Hulten's *Flora of Alaska and Yukon* (1941) was used as the source for vascular plant distribution records. It is realized that Hulten's comprehensive work does not include all Alaskan species, nor are ranges as completely known as would be desirable. There are many areas within this vast state where few botanical collections have been made; range extensions and adjustments are being recorded annually. Yet, even within the limitation of knowledge concerning the flora of Alaska, the general trends and salient features should be little affected by addition of a few species or minor range adjustments.

Alaska can be divided into five subregions (exclusive of Kodiak) for purposes of grouping plant distribution records. These subregions are:

- Southeastern Alaska (northwestward to Yakutat)
- Kenai Peninsula-Cook Inlet area
- Alaska Peninsula (Iliamna to Cold Bay)
- Aleutian Islands
- Interior Alaska (all Alaska north and east of Bristol Bay and the Alaska Range)

Each of these subdivisions is a fairly well naturally defined unit, except for the large interior region. This area encompasses nearly all of the true arctic and much of the boreal zone in Alaska. Those species recorded by Hulten from southwestern Yukon were included in the interior subregion, for this area is the geographic connection between interior and southeastern Alaska.

In this study species that have been recorded

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from Kodiak Island were tabulated along with each of the other subregions in which the species have also been recorded. This resulted in determining the total number of plant species on the Kodiak Island Group and in what other parts of Alaska the same species occurred. Interpretation of these data needs qualification in order to allow for a discontinuous distribution or for a hiatus in distributional records. A situation of this nature arises because only intra-Alaska distribution was considered. To illustrate: if a species was not recorded from the southeastern region but was found in the remainder of Alaska, it would appear that the species in question was a northern form, but this species could range along the British Columbia or Washington coasts. Thus, an erroneous conclusion could result from considering only intra-Alaskan ranges. However, for consistency, distribution outside of Alaska and the southwestern part of Yukon was not considered in the compilation of the subregional plant lists.

PHYSICAL FEATURES

Geologically, the Kodiak Archipelago is a continuation of the Kenai Peninsula 40 miles to the northeast. Separating the islands from the Alaska Peninsula on the northwest is the 20–30-mile wide and 600-plus-ft-deep Shelikof Strait. Fourteen islands larger than 7 sq miles make up the 4,900 sq miles of land in the archipelago. Kodiak is much the largest with 3,588 sq miles, and Afognak, with 700 sq miles, is second. This Island Group extends for approximately 180 miles in a northeast-southwest direction (Fig. 1).

The oldest rocks are Triassic and Jurassic, but overlying these are thick series of slate, graywacke, and conglomerates of late Mesozoic Age. More recent are deposits of sandstones and shales (Capps, 1937). The area was a center of extreme glaciation as local glaciers pushed seaward from all directions and as extremities of Peninsular and Kenai glaciers reached the Island Group. An intricate fjord coastline resulted from this glaciation.

Relief is irregular, with peaks rising to 4,000 ft on Kodiak Island and 2,200 ft on Afognak Island.

The temperate climate is uniformly cool, with a well-distributed annual precipitation of ap-

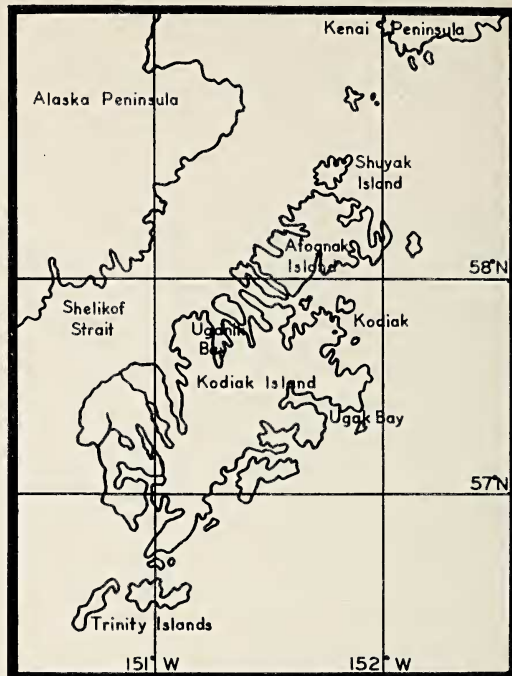


FIG. 1. Outline map of the Kodiak Archipelago.

proximately 60 inches. Maximum air temperatures are in the low 80's and minimums seldom go below 0° F (Capps, 1937).

A layer of volcanic ash from the 1912 eruption of Mount Katmai covered much of the Island Group with up to several inches of pumice. Griggs (1915, 1918) and Wilcox (1959) discussed the influence of this and subsequent volcanic ash falls on vegetation.

VEGETATION

The Pacific Coastal Forest reaches its most northwesterly extension on Kodiak Island. Shuyak and Afognak islands are discontinuously forested at elevations below 700 ft. Outliers of this coastal forest extend north and south across Kodiak Island from Uganik Bay to Ugak Bay. To the immediate northward, along the base of the Alaska Peninsula, there are also small sections of coastal forest.

Dominating the forest is *Picea sitchensis* (Bong.) Carr., the only conifer on the archipelago. The open understory consists of *Vaccinium ovalifolium* Smith, *Oplopanax horridus* (Sm.) Migs., and *Rubus spectabilis* Pursh.

There seems to be little doubt but that *Picea*

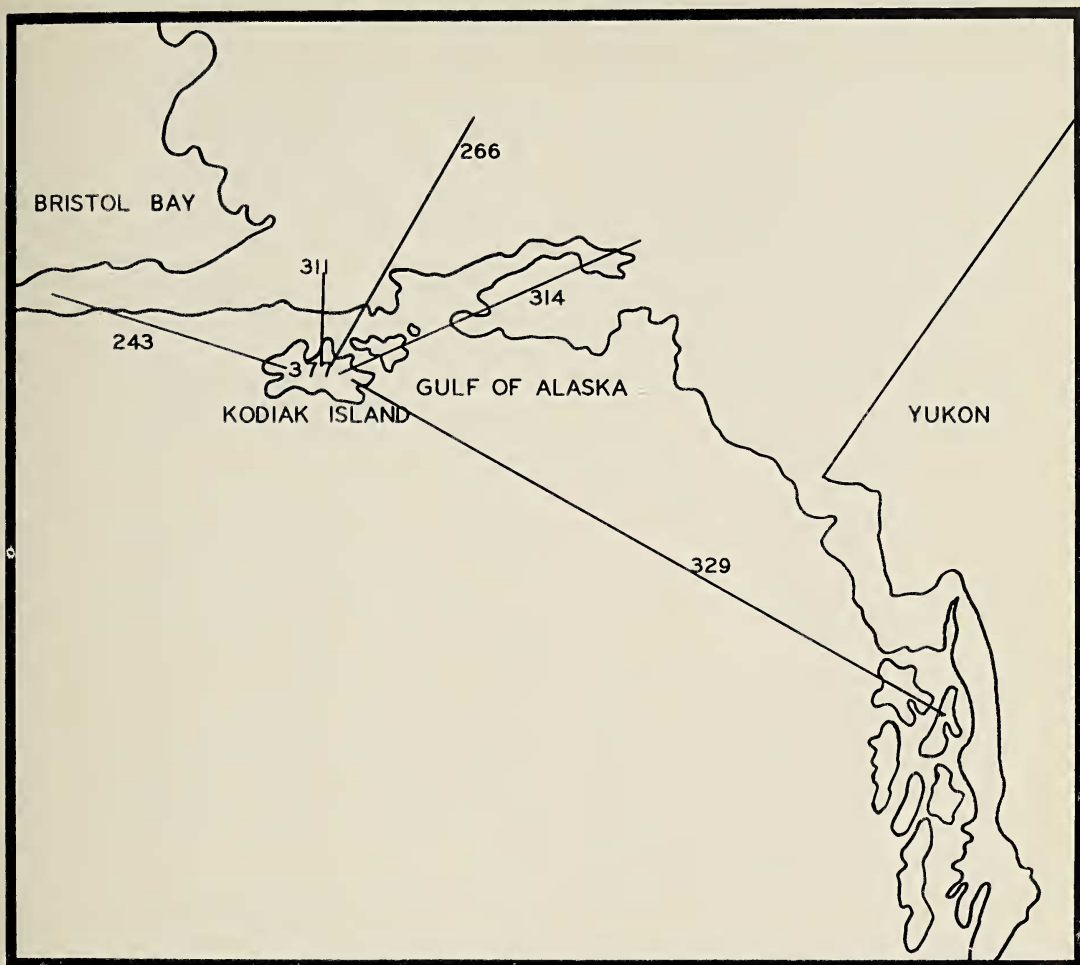


FIG. 2. The number of plant species on Kodiak Island that are also found in other regions of Alaska.

forest is extending its range. Pollen analysis, historical records, tree growth, and tree age all indicate the recent advance of the forest border in the area near the village of Kodiak (Bowman, 1934; Griggs, 1934a, 1946; Heusser, 1960). No evidence has been reported that showed a more northward or westward conifer treeline during the hypsithermal. As Aleksandrova (1960) found on Novaya Zemlya, coniferous trees probably had not yet reached the Kodiak Island Group by the period of thermal maximum.

Calamagrostis canadensis (Michx.) Beauv. and *Alnus crispa* (Ait.) Pursh. that appear in the *Picea* forest openings become the characteristic plant cover for the southwestern part of

Kodiak Island. Nearly all well-drained sites are occupied by this plant combination, which Griggs (1936) classified as subclimax in the nearby Katmai district. Hulten (1960) described this *Alnus-Calamagrostis-Streptopus* vegetation of western coastal Alaska as similar to that of some sections of Kamtchatka. Superimposed on this vegetation along stream valleys is *Populus trichocarpa* Torr. and Gray. Other shrubs which commonly appear are *Betula nana* L., *Vaccinium vitisidea* L., and *Empetrum nigrum* L. Abundant grasses are *Hordeum brachyantherum* Nevski., *Elymus mollis* Trin., *Eriophorum angustifolium* Roth, and *Hierochloe alpina* (Sw.) Roem. and Schult. Twenty-six species of *Carex* are found

on the Island Group. Mosses and lichens which are important in many tundra areas are of minor importance on western Kodiak Island, but eastward mosses form a prominent ground cover under the spruce forest.

Although the Kodiak tundra-like area has many affinities with the more northern tundras, it should not be considered a true tundra. As is characteristic of many northern vegetation types, it is not the species present that are characteristic but the relative abundance of each. Griggs (1934*b*, 1936) discussed this problem in regard to the Katmai district of the Alaska Peninsula. Kodiak Island is the only place in North America where the Arctic Zone is not bordered on the south by the boreal forest. In this area arctic or quasi-arctic vegetation makes direct contact with the temperate coastal forest.

THE FLORA AND ITS RELATIONSHIP TO OTHER REGIONS

Hulten recorded 377 species of vascular plants from the Kodiak Island Group. Of these same plants 329 are also found in southeastern Alaska; 314 in the Kenai-Cook Inlet area; 311 in the Alaska Peninsula; 243 in the Aleutians; and 266 in interior Alaska (Fig. 2). These total figures strongly indicate that all sections of Alaska have contributed to the flora of Kodiak. Of the total Kodiak flora, 156 species are found in all of the five designated subregions; and 132 more species are in all of Alaska except one subregion. As with most northern floras (Porsild [1951] stated that one-third of the North American arctic plants are circumpolar), that of Kodiak is dominated by holarctic or at least nearctic species. The sharpest break in the flora is with the Aleutians; 62 species which are found on Kodiak Island are also in all Alaska except the Aleutians. Phytogeographically, much of the Aleutians belongs to Kamtchatka (Hulten, 1960), but the remainder of Alaska is North American.

Following the previous division, the Alaska distribution of the Kodiak flora can be grouped into eight types of distributions. These are listed along with a few representative examples.

1. Throughout all Alaska (156 species): *Equisetum arvense* L., *Loiseleuria procumbens* (L.) Desv., *Oxyria digyna* (L.) Hill., *Empetrum nigrum* L., *Saxifraga oppositifolia* L.

2. All Alaska except Kenai-Cook Inlet (13

species): *Agrostis borealis* Hartm., *Carex stylosa* C. A. Mey., *Ranunculus repens* L.

3. All Alaska except Aleutians (62 species): *Thalictrum sparsiflorum* Turcz., *Andromeda polifolia* L., *Sambucus racemosa* L.

4. All Alaska except Southeastern (15 species): *Lagotis glauca* Gaertn., *Saxifraga bracteata* D. Don., *Phyllodoce aleutica* (Spreng.) A. Heller.

5. All coastal areas of Alaska (42 species): *Puccinellia nutkaensis* (Presl.) Fern and Weath., *Rubus spectabilis* Pursh., *Poa stenantha* Trin.

6. Only in Kodiak and regions eastward (50 species): *Lysichitum americanum* Hult. and St. J., *Juncus oregonus* S. Wats., *Spergularia canadensis* (Pers.) G. Don.

7. Only in Kodiak and regions northward (13 species): *Juncus triglumis* L., *Rumex arcticus* Trautv., *Cicuta mackenzieana* Raup.

8. Only in Kodiak and regions westward (13 species): *Plagiobothrys orientalis* (L.) Johnston., *Taraxacum trigonolobium* Dahlst., *Euphrasia mollis* (Ledeb.) Wettst.

If we examine the latter three of the above groups (the others have too wide a distribution to denote an affinity pattern), further indication may be apparent as to the relationship of the flora of Kodiak Island to the remainder of Alaska.

There are three general directions from which plants could reach the Kodiak Island Group: (1) from the west via the Aleutians and through the Alaska Peninsula, (2) from the northern interior by way of the Alaska Peninsula and the Kenai Peninsula, and (3) from the southeast out of southern Alaska, again by way of the Kenai Peninsula and the Alaska Peninsula. Ocean currents could also be a factor, as the Gulf of Alaska Current runs in an arcuate path from southeastern Alaska past Kodiak Island (Fig. 3).

Of the species whose ranges in Alaska are applicable, 50 came from the east and 13 each from the north and west. The diversity of possible elements from the southeast should not be overlooked. There are montane, coastal, boreal, and some arctic elements available from this direction.

Seven species are listed by Hulten with an Alaskan range of only Kodiak Island. This apparent endemism is probably due to a lack of data, for Anderson (1959) listed several of

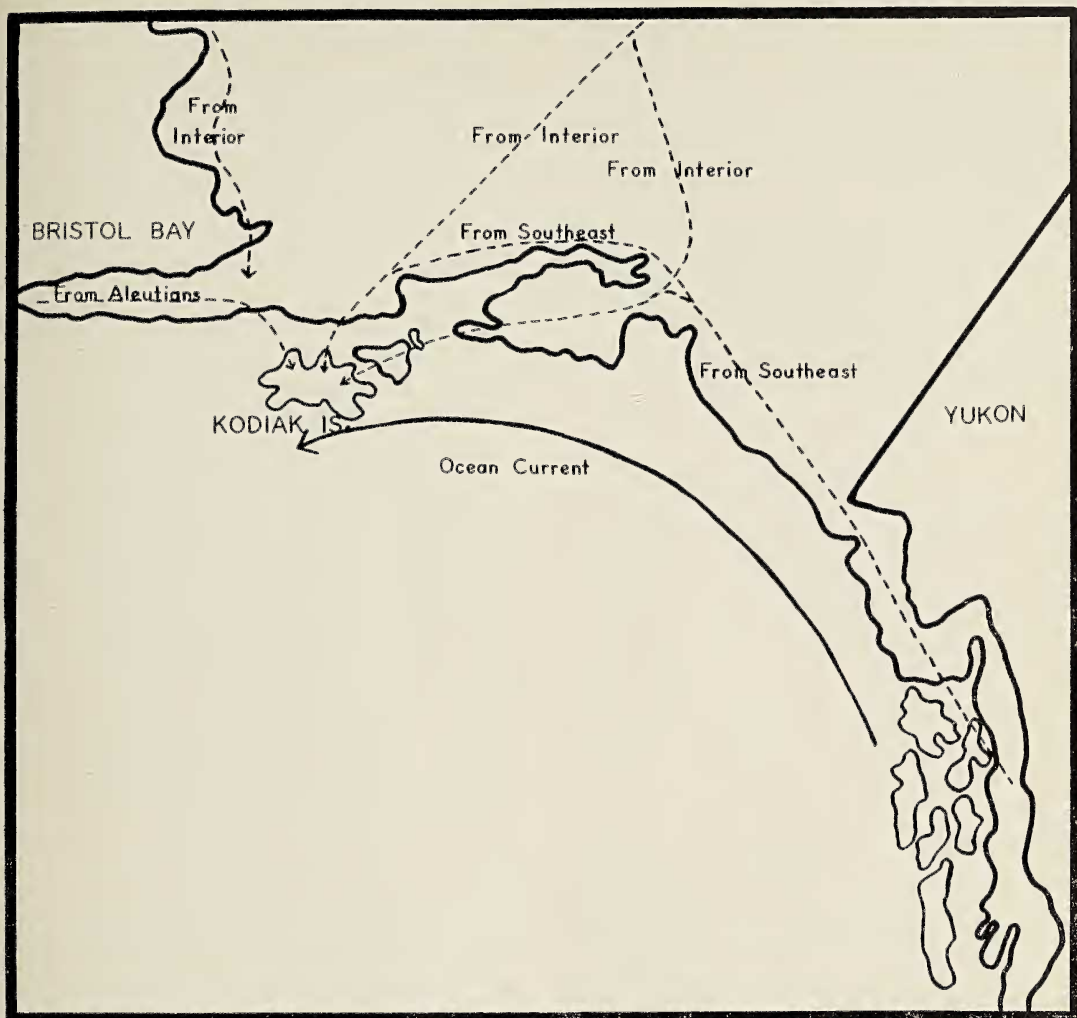


FIG. 3. Schematic presentation of available direction and routes of migration to Kodiak Island.

these same species as being fairly widespread throughout coastal Alaska.

Further insight regarding affinity of the Kodiak flora may be found by examining some of the characteristic species and the elements with which they are commonly associated.

Three species are found that are typical of both Asiatic and American sectors of the North Pacific. They are *Fritillaria camtschatcensis* (L.) Ker., *Oplopanox horridus* (Sm.) Mig., and *Casiope lycopodioides* (Pall.) D. Don.

The arctic tundra is represented by such species as *Luzula nivalis* (Laest.) Beurl., *Cardamine bellidifolia* L., *Empetrum nigrum* L., *Arctostaphylos alpina* (L.) Spreng., *Hierochloa alpina*

(Sw.) Roem and Schult., *Betula nana* L., *Alnus crispa* (Ait.) Pursh., *Carex aquatilis* Wahl., *Lycopodium selago* L., and *Saxifraga hirculus* L.

Petran tundra has such characteristic species present as *Carex pyrenaica* Wahl., *C. nigricans* C. A. Mey., *Androsace chamaejasme* Host., and *Thalictrum alpinum* L. There are eight species of *Poa*, four species each of both *Agrostis* and *Luzula*, as well as representatives of *Festuca*, *Phleum*, and *Trisetum*.

The widespread arctic-montane species: *Polygonum viviparum* L., *Oxyria digyna* (L.) Hill., and *Saxifraga oppositifolia* L. are also present.

The boreal forest element consists of such species as *Vaccinium uliginosum* L., *V. vitis-*

idaea L., *Viburnum edule* (Michx.) Raf., *Pedicularis labradorica* Panzer., *Cornus canadensis* L., and *Calamagrostis* sp.

Coastal forest species are: *Picea sitchensis* (Bong.) Carr, *Vaccinium ovalifolium* Smith, *Oplopanax horridus* (Sm.) Mig., and *Rubus spectabilis*, Pursh.

Conspicuous by their absence from Kodiak, yet present in adjoining regions or throughout Alaska are: *Poa arctica* R. Br., *Arctagrostis latifolia* (R. Br.) Griseb., *Draba nivalis* Lilj., *Sagina intermedia* Fenzi., *Picea glauca* (Moench) Voss., and *Astragalus alpinus* L.

ANIMAL DISTRIBUTION

An interesting zoogeographical situation arises in regard to the land mammals. Only six species are known to be native to the Island Group (*Myotis lucifugus*, *Microtus oeconomus*, *Vulpes fulva*, *Ursus middendorffi*, *Mustela erminea*, and *Lutra canadensis*). At least 12 introduced mammals have become established. Many of these introduced mammals as well as others not present are common on the nearby mainland but have not become naturally established on the islands.

The indigenous mammals have affinities with several regions. *U. middendorffi* is closely related to the Asiatic bears. *M. lucifugus* is a widely-distributed more southerly form. *M. oeconomus* is typically a northern meadow mouse. The remaining three native species have a general circumpolar distribution or else a closely related palaeartic counterpart. Many of the introduced species are either more southern forms or boreal species. The near absence of the expected boreal mammals is conspicuous. All native mammals could have easily moved from the mainland to the islands either by flight or swimming, or were small enough to be transported by drift.

Thus, mammals show much the same affinity pattern as plants: a dominance of holarctic forms, with the remainder of the fauna having strong relationships to Asia, the Arctic, and more southerly regions. Introduced species from the boreal and coastal forests thrive. As in plants, mammals not expected to have been found in Beringia appear to have been late in arriving on the Island Group or have invaded the islands only with man's help.

The avifauna appears to be drawing its members from four areas: Asiatic immigrants, such as *Branta nigricans* and *Larus hyperboreus*; Bering Sea immigrants, as *Aethio cristatella* and *Fratercula corniculata*; northern immigrants, as *Gavia stellata* and *Lagopus lagopus*; southeastern immigrants, as *Megasceryle alcyon* and *Ixoreus naevius*; and numerous widespread holarctic species. Williamson and Peyton (1962) found five species of birds in the nearby Iliamna area that possessed characteristics intermediate between interior and coastal populations. However, the avifauna of this region differs from the biota of Kodiak Island in that an Hudsonian avifauna dominates.

All freshwater fishes on the Island Group are euryhaline. Members of each species move readily back and forth between fresh and salt-water. The wide-ranging north temperate *Gasterosteus aculeatus*, the five species of the North Pacific genus *Oncorhynchus*, the more southerly *Salmo gairdneri*, *Cottus aleuticus* with its range centered in the Aleutians, and two charrs (*Salvelinus malma*, a southern species, and *S. alpinus*, an arctic species), whose range overlap on Kodiak Island, collectively present an affinity pattern similar to that of the plants.

DISCUSSION

Climatic similarity is encouraging the expression of southeastern elements. The atypical arctic element may be due to this same maritime temperate climate and proximity of the Island Group to the large unglaciated portion of northwestern Alaska. Re-immigration has not proceeded as rapidly as climatic change; thus, a gap exists between current and seemingly potential distribution. In the case of mammals, this gap is being closed rapidly by introduction. The Kodiak region is characterized by the northward advancement of the temperate coastal elements into an area now occupied by a heterogeneous biota. Boreal elements, both plant and animal, that normally occupy this region are much reduced.

Although Kodiak latitudinally belongs in the Boreal Zone, boreal elements are not as well represented as arctic, montane, or coastal elements. Poor boreal expression may stem from the barrier formed by the Rocky Mountain complex between the boreal areas. The effective-

ness of this barrier is suggested by the number of plant species (13) found in all regions of Alaska (including Kodiak) except the Kenai-Cook Inlet area and the marked individuality of the coastal forest. In the absence of boreal expression, coastal forests elements extend farther north into arctic situations in order to occupy this habitat. In addition, approximately 20 common boreal mammals that have not made their way by natural means to the Islands are found on the nearby Alaska mainland. This again indicates late arrival of this group of mammals in southwestern Alaska.

Abundance of arctic plant elements may be the result of the archipelago being closer to the Beringian refuge than it was to the more continental boreal region. A reservoir of arctic plant species was available to invade the denuded temperate islands (Hulten [1937] said that nearly all plants west of Prince William Sound originated in Beringia), whereas many boreal plant and animal species had to migrate from southern refuges, occupying much of the present Boreal Zone before reaching Kodiak. In place of a mountain barrier to surmount, arctic species could follow the Bering Sea coastal plain. This same mountain complex, which is a barrier to boreal species, probably accounts for the prevalence of Petran tundra species. Coastal forest species, on the other hand, could utilize the exposed coastal plain as a migration route from the Washington-Oregon refuge area.

The information presented in this paper establishes that the Kodiak Archipelago is drawing members for its youthful biota from several sources, namely, Asia via the Aleutians and Bering Strait, interior and arctic Alaska, and southeastern Alaska. Boreal biota is largely lacking due to mountain barriers and distance to late Pleistocene refuges utilized by boreal species. Favored by the prevailing climate, coastal forest elements are expanding over the archipelago. There is little evidence to suggest that the refuge area on southwestern Kodiak Island was an important center of dispersal.

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